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# A FIRST STUDY OF THE INFLUENCE OF THE STARVATION OF THE ASCENDANTS UPON THE CHARACTERISTICS OF THE DESCENDANTS—I

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## I. INTRODUCTORY REMARKS

ONE need not search widely in biological or agricultural literature to encounter discussions of the influence of the conditions to which the ancestors are exposed upon the characteristics of the offspring which they produce. To review here the mass of more or less pertinent literature would lead us too far afield from our present main purpose, which is simply to present the data and state the apparent conclusions from an experimental and statistical study of the influence of starvation and feeding upon the characteristics of garden beans. It is sufficient for the moment to point out that some biologists have attributed a very important rôle to the environment of the mother in determining the characteristics of the offspring. It is perhaps superfluous to say that others of equal authority have expressed diametrically opposite opinions.

The problem is, therefore, a real and an important one. Unfortunately the serious investigator who publishes in this field is sure to be between two large and several

smaller fires. If after cultures of a few generations he finds that the offspring of starved parents do not differ from those which have been well fed, he will be railed at for having wasted his time in demonstrating what was obvious in advance. At the same time he will be criticized by others for not having carried out his experiments "for a sufficient number of generations to allow the accumulation of small effects of the environment" on the ascendants before deciding against the possibility of some influence upon the descendants of ancestral environmental conditions. If he finds that there are measurable differences between series of individuals whose ancestry has been subjected to opposed conditions, the results are sure to be dismissed in many quarters as of little importance because of purely physiological and not hereditary significance.

The very fact of the inevitability of criticism—whatever the results obtained—seems to render it even more highly desirable to appeal to the facts afforded by a large and detailed experimental investigation. Naturally such an experiment can never be so large and so refined as to be beyond all criticism.

The problem is not merely of wide interest from the purely biological viewpoint, but it is of first rate importance from the practical side as well. The biggest pumpkin, the heaviest bull, and the finest ear of corn are the resultant of germ plasm and environment—of nature and nurture, to use Galton's apt words. But in paying fabulous prices for the seed of prize winners little thought is given to the question of the proportionate importance of breeding and feeding in producing this excellence. From the practical standpoint it seems desirable to know whether parents—animals or plants—of as nearly as possible the same hereditary endowment differ at all in their capacity for producing high-grade offspring because of the superior care and feeding which admits them to the show bench. If it be found that the well-fed mother produces finer, or poorer, offspring than the starved one, the practical significance of the result is obvious and the

further biological problems of the nature and permanence of this influence will be open for investigation.

Finally it may be said in passing that the work on these beans was so carried out that data for many other problems besides those discussed here were secured. That of the pure line, that of the relationship between the size of the seed planted and the characteristics of the plant produced, that of the relationship between the size of the plant and the fertility of its pod and the size of the seeds which it produces, that of the relationship between the ovule characters of the pod and its fertility, may be mentioned. These will shortly be made ready for publication; hence if the reader encounters these series of beans in several different places he must not assume duplicate publication. The mass of data in hand is so great that it is either necessary to scatter the material in this way or to withhold it all for several months or years until it can be presented in one volume. The former scheme for several reasons seems the most expedient.

## II. Statement of Problems and Description of Materials and Methods

### *A. Limitation of the Problem*

The purpose of this paper is to present the results of a series of experiments to determine whether plants whose ancestors have been starved differ from those whose ancestors have been well fed.

It might seem to the reader that the first step in such a problem would be to define starvation and feeding, to list the factors underlying these conditions, and to ascertain the weight of each of these factors in determining the characteristics of a series of plants subjected to them.

This seemed to me in undertaking these particular experiments precisely the course which one should not follow. Physiologists, especially those concerned with plant nutrition in the agricultural stations, have devoted a quarter of a century or more to these very problems.

But concerning the influence of the feeding or starving of the parent upon the characteristics of the offspring, we have little direct experimental knowledge.

It seemed expedient therefore to neglect for the moment the problem of the various edaphic and metereological factors which determine the characteristics of the individual and to ascertain whether the subjecting of parent plants (or parents and earlier ascendants) to differing environmental conditions has any influence upon the characteristics of the offspring. It was therefore only necessary to find fields in which the soil barely sustained a given variety and others which produced a luxuriant growth. The first would represent for the species in question starvation fields.

The judgment of the relative richness of the plots by their actual productiveness is justified by our ignorance of the nature of soil fertility.

The reader who is inclined to criticize this method of approaching the problem as very coarse may be reminded of the following points:

(*a*) The complexity of the problem of soil fertility is such as to preclude a trustworthy evaluation of the particular factors determining the productiveness of any parcel of ground.[1] For this reason I have purposely omitted all but the barest descriptions concerning the experimental plots employed.

(*b*) Artificial soils or water culture media of known chemical composition were carefully considered and ruled out. In the first place, the technical difficulties seemed almost unsurmountable. Again, it seemed desirable to carry on the experiments under conditions as nearly as possible identical with those to be met with in practical agriculture. Chemically prepared nutrient solutions are useful in the physiological laboratory, but they do not occur in practical farming, while soils which are "sterile"

[1] Soil experts now agree that chemical analyses of soils furnish no sure criterion of their productiveness.

and those which are "productive"—for what reason we do not know—do.[2]

The solution of our problem is to be sought by means of a series of comparisons which fall into two classes. The first is designed to test the influence of the environment upon the characteristics of the individual; the second is intended to show what influence, if any, the treatment of the ancestors has had upon the offspring.

The first series of comparisons is essential in that it brings out clearly the extent to which the ancestors were modified by the environment to which they were subjected. It affords no evidence whatever as to the factors to which these effects are due. The second set of comparisons is the important one. Our problem, the reader must distinctly understand, is not to determine why some individuals are depauperate and others luxuriant, but whether the rendering of individuals depauperate through the environment to which they are subjected has any influence upon the measurable characteristics of their offspring.

## *B. Material*

The materials upon which this study was based were furnished by five series of garden beans, *Phaseolus vulgaris*. Two of these were the common white Navy. The third was a strain of Burpee's Stringless first grown from commercial seed at the Missouri Botanical Garden in 1905. The other two were from the seed of the White Flageolet and Ne Plus Ultra which Dr. Shull had used in his hybridization experiments.[3]

[2] Our great ignorance of the problem of soil fertility is attested by the words of Professor Hall in a chairman's address before the Sheffield meeting of the British Association (*Science*, N. S., Vol. 32, p. 364, 1911). He said:

"The fertility of the soil is perhaps a vague title, but by it I intend to signify the greater or less power which a piece of land possesses of producing crops under cultivation, or, again, the causes which make one piece of land yield larger crops when another piece alongside only yields small ones, differences which are so real that a farmer will pay three or even four pounds an acre rent for some land, where he will regard the other as dear at ten shillings an acre."

[3] Shull, G. H., *Science*, N. S., Vol. 25, pp. 792–794, 828–832, 1907; AMER. NAT., Vol. 42, pp. 433–451, 1908.

The two Navy series first came to my attention on the farms of George A. Harris and Elmer Dille at Mount Hermon, near Plantsville, Athens Co., Ohio, in the fall of 1907. From the Harris farm 160 plants were taken, giving rise to 160 "pure lines." These are the Navy *H*, or *NH* series. From the Dille field 550 plants were taken

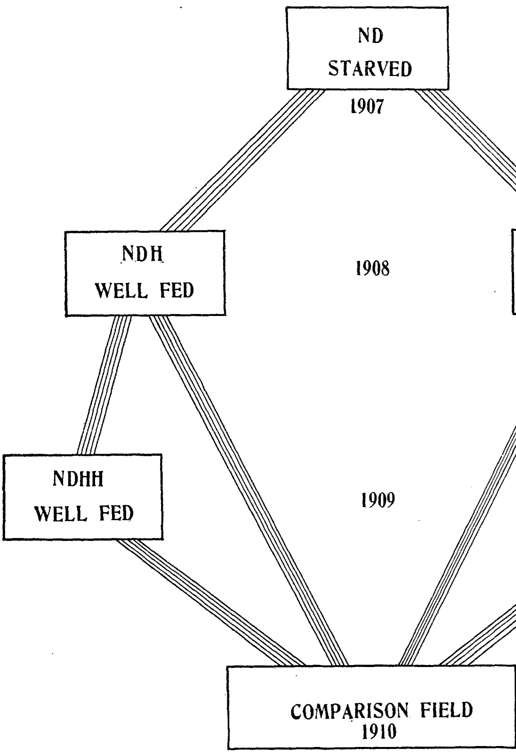



Diagram I. Cultural history of the Navy D series. The history of the Navy H series is the same, and can be expressed by substituting H for D as the first habitat letter in the formulæ.

and yielded 550 "pure lines," designated as the Navy *D* series. These two fields furnished, as explained in detail in a subsequent section, the starvation and feeding tracts of the experiment.

Dr. Shull's seeds saved for individual plants of a crop of 1907 yielded 80 lines of Ne Plus Ultra and 100 of White Flageolet.

The history of these strains during the course of the

experiment is shown by the diagrams. The seriations of number of pods per plant appear in the Data Tables *A*, *B* and *C*.

TABLE *A*

PODS PER PLANT

| Series | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | Total Plants |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *D* | 55 | 229 | 165 | 63 | 24 | 8 | 4 | 1 | 1 | — | — | — | — | — | — | — | 550 |
| *DD* | 46 | 107 | 141 | 89 | 57 | 36 | 16 | 11 | 3 | 4 | 2 | — | — | 1 | — | — | 513 |
| *DDD* | 10 | 61 | 93 | 107 | 67 | 55 | 31 | 24 | 5 | 4 | — | 1 | 1 | — | — | — | 459 |
| *HD* | 92 | 235 | 333 | 282 | 192 | 135 | 81 | 38 | 11 | 6 | 7 | 1 | 1 | 2 | — | — | 1,416 |
| *HDD* | 49 | 172 | 234 | 208 | 204 | 119 | 84 | 51 | 34 | 22 | 9 | 9 | 3 | 3 | 2 | 1 | 1,204 |
| *USD* | 53 | 111 | 95 | 30 | 12 | 8 | 3 | — | — | — | — | — | — | — | — | — | 312 |
| *USDD* | 25 | 64 | 42 | 34 | 33 | 19 | 12 | 3 | 1 | 2 | 1 | — | — | — | — | 1 | 237 |
| *FSD* | 39 | 100 | 118 | 76 | 43 | 26 | 12 | 13 | — | 1 | — | — | — | — | — | — | 428 |
| *FSDD* | 13 | 52 | 98 | 91 | 64 | 43 | 15 | 4 | 4 | 1 | — | 1 | — | 1 | — | — | 387 |

For convenience of reference I designate the 1907, 1908 and 1909 cultures the ancestral series and the 1910 crops the comparison series. The fitness of these terms will be apparent.

## *C. Experimental Methods and Collection of Data*

Experimental methods may conveniently be explained under three heads: Selection and Care of Seed, Cultural Conditions, and Collection of Data.

### 1. Selection and Care of Seed

The necessary requirements are two. First, it is essential that the material subjected to the various environmental factors shall be identical in its hereditary tendencies. Second, it is essential that in the routine of growing, harvesting and planting no purely physiological (as contrasted with hereditary, germinal or genetic) sources of differentiation shall be introduced.

Consider the first requirement.

We have learned from both biometric and Mendelian researches that it is impossible to know from the simple inspection of an apparently uniform group of individuals whether or not they are really identical as to germinal constitution. It is therefore idle to plant seeds of some individuals under starvation and seeds of other individ-

TABLE *B*

NUMBER OF PODS PER PLANT

| Series | *H* | *HH* | *HHH* | *DH* | *DHH* | *USS* | *USH* | *USHH* | *FSS* | *FSH* | *FSHH* |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | — | 7 | 4 | 9 | 4 | — | — | — | 4 | — | — |
| 2 | — | 8 | 10 | 10 | 6 | — | 1 | 3 | 5 | 1 | 6 |
| 3 | 1 | 10 | 20 | 16 | 9 | 2 | 2 | 6 | 12 | 4 | 5 |
| 4 | 4 | 11 | 36 | 21 | 12 | 2 | 5 | 11 | 21 | 4 | 11 |
| 5 | 3 | 25 | 52 | 20 | 10 | 3 | 5 | 15 | 24 | 9 | 9 |
| 6 | 4 | 34 | 62 | 20 | 26 | 6 | 8 | 26 | 24 | 6 | 20 |
| 7 | 6 | 41 | 78 | 29 | 39 | 16 | 15 | 27 | 25 | 14 | 26 |
| 8 | 7 | 55 | 91 | 26 | 42 | 17 | 20 | 38 | 38 | 12 | 34 |
| 9 | 10 | 58 | 82 | 36 | 43 | 30 | 17 | 28 | 43 | 22 | 32 |
| 10 | 12 | 97 | 94 | 43 | 52 | 48 | 40 | 23 | 67 | 32 | 31 |
| 11 | 9 | 76 | 91 | 35 | 51 | 49 | 17 | 15 | 34 | 24 | 33 |
| 12 | 12 | 78 | 96 | 39 | 37 | 54 | 22 | 12 | 43 | 22 | 42 |
| 13 | 12 | 94 | 115 | 34 | 47 | 48 | 28 | 7 | 65 | 22 | 40 |
| 14 | 9 | 74 | 88 | 34 | 40 | 49 | 25 | 3 | 47 | 24 | 34 |
| 15 | 7 | 72 | 60 | 28 | 35 | 52 | 23 | 3 | 50 | 25 | 25 |
| 16 | 7 | 83 | 72 | 35 | 19 | 37 | 26 | 3 | 42 | 23 | 16 |
| 17 | 9 | 69 | 52 | 35 | 22 | 49 | 18 | 1 | 37 | 19 | 10 |
| 18 | 8 | 66 | 39 | 30 | 12 | 32 | 13 | 1 | 46 | 27 | 13 |
| 19 | 5 | 56 | 29 | 24 | 17 | 32 | 20 | — | 31 | 19 | 13 |
| 20 | 1 | 56 | 25 | 21 | 11 | 26 | 13 | — | 36 | 17 | 10 |
| 21 | 4 | 51 | 25 | 16 | 5 | 18 | 12 | — | 42 | 19 | 7 |
| 22 | 3 | 41 | 12 | 9 | 7 | 22 | 6 | — | 23 | 12 | 2 |
| 23 | 5 | 46 | 8 | 13 | 4 | 20 | 3 | 2 | 14 | 23 | 3 |
| 24 | 3 | 37 | 7 | 11 | 3 | 12 | 5 | — | 12 | 8 | 2 |
| 25 | 2 | 28 | 6 | 5 | 6 | 16 | 4 | — | 11 | 11 | 1 |
| 26 | 2 | 27 | 6 | 8 | 4 | 10 | 2 | — | 16 | 12 | 1 |
| 27 | 2 | 19 | 1 | 9 | 2 | 7 | 3 | — | 9 | 12 | 2 |
| 28 | 4 | 12 | 2 | 7 | — | 4 | 5 | — | 4 | 13 | — |
| 29 | 1 | 14 | 1 | 10 | — | 2 | 1 | — | 7 | 7 | — |
| 30 | 2 | 23 | 2 | 5 | — | — | 1 | — | 8 | 2 | — |
| 31 | 1 | 20 | — | 2 | — | 5 | — | — | 5 | 6 | — |
| 32 | — | 12 | 3 | 3 | — | 1 | — | — | 2 | 2 | — |
| 33 | — | 10 | — | 5 | — | 3 | — | — | 2 | 4 | — |
| 34 | 1 | 10 | 2 | 3 | — | 1 | — | — | 4 | 3 | 1 |
| 35 | — | 11 | — | 3 | — | 1 | — | — | 2 | 4 | — |
| 36 | 1 | 4 | — | 2 | — | — | — | — | 1 | 1 | — |
| 37 | 1 | 7 | — | 4 | — | 2 | — | — | 4 | 3 | — |
| 38 | — | 6 | — | 3 | — | — | — | — | — | 1 | — |
| 39 | — | 5 | — | 1 | — | 1 | 1 | — | 1 | — | — |
| 40 | 1 | 5 | — | 1 | — | 1 | — | — | — | 1 | — |
| 41 | — | 3 | — | — | — | — | — | — | — | 2 | — |
| 42 | — | 2 | — | 1 | — | — | — | — | 1 | — | — |
| 43 | — | 3 | — | — | — | — | — | — | 2 | 1 | — |
| 44 | — | 1 | — | — | — | — | — | — | — | 1 | — |
| 45 | — | 2 | — | 1 | — | — | — | — | 1 | — | — |
| 46 | 1 | 5 | — | — | — | — | — | — | — | — | — |
| 47 | — | 1 | — | — | — | — | — | — | — | — | — |
| 48 | — | — | — | 1 | — | 2 | — | — | 1 | — | — |
| 49 | — | 1 | — | 1 | — | — | — | — | — | 1 | — |
| 50 | — | — | — | 1 | — | — | — | — | — | — | — |
| 51 | — | 1 | — | — | — | — | — | — | — | — | — |
| 52 | — | 2 | — | — | — | — | — | — | 1 | — | — |
| 54 | — | 2 | — | — | — | — | — | — | 1 | — | — |
| 55 | — | 1 | — | — | — | — | — | — | — | — | — |
| 56 | — | 1 | — | — | — | — | — | — | — | — | — |
| 67 | — | 1 | — | — | — | — | — | — | — | — | — |
| Total plants | 160 | 1,484 | 1271 | 670 | 565 | 680 | 361 | 224 | 868 | 475 | 429 |

uals of apparently the same uniform variety under feeding conditions. The only certain method of securing the

TABLE *C*

NUMBER OF PODS PER PLANT

| Series | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *HHC* | 8 | 8 | 16 | 26 | 35 | 30 | 25 | 31 | 30 | 46 | 25 | 23 | 23 | 21 | 28 | 14 | 18 | 5 | 9 | 8 | 12 | 12 | 11 | 4 | 4 | 2 | 3 |
| *HHHC* | 8 | 13 | 20 | 34 | 41 | 48 | 38 | 35 | 43 | 37 | 26 | 36 | 25 | 24 | 19 | 17 | 10 | 14 | 15 | 8 | 10 | 8 | 5 | 3 | 4 | 2 | 3 |
| *HDC* | 6 | 10 | 25 | 26 | 29 | 30 | 26 | 28 | 25 | 14 | 12 | 11 | 16 | 23 | 16 | 9 | 10 | 11 | 5 | 5 | 7 | 5 | 4 | 4 | 2 | 3 | — |
| *HDDC* | 11 | 15 | 23 | 35 | 36 | 35 | 32 | 43 | 28 | 34 | 19 | 29 | 32 | 17 | 17 | 10 | 19 | 13 | 15 | 6 | 5 | 4 | 4 | 4 | 1 | 3 | 2 |
| *DDC* | 6 | 16 | 12 | 12 | 20 | 22 | 26 | 14 | 18 | 16 | 8 | 16 | 15 | 15 | 8 | 7 | 4 | 5 | 6 | 1 | 2 | 1 | 1 | — | 1 | 1 | — |
| *DDDC* | 6 | 10 | 14 | 23 | 30 | 27 | 27 | 21 | 22 | 23 | 21 | 18 | 16 | 16 | 8 | 6 | 6 | 7 | 3 | 7 | 2 | 1 | 2 | 4 | 2 | 1 | — |
| *DHC* | 9 | 21 | 19 | 35 | 41 | 34 | 32 | 33 | 29 | 34 | 25 | 18 | 15 | 13 | 16 | 10 | 8 | 11 | 13 | 7 | 5 | 1 | 7 | 2 | 2 | 1 | — |
| *DHHC* | 7 | 17 | 30 | 38 | 45 | 40 | 52 | 40 | 38 | 34 | 27 | 27 | 19 | 11 | 17 | 19 | 14 | 10 | 9 | 10 | 6 | 1 | 4 | 4 | 4 | 2 | 4 |
| *USC* | 3 | 5 | 15 | 22 | 25 | 31 | 48 | 50 | 53 | 69 | 37 | 28 | 31 | 30 | 29 | 15 | 10 | 6 | 6 | 5 | 3 | 2 | 1 | 2 | 1 | 1 | 2 |
| *USSC* | 1 | — | 5 | 8 | 10 | 21 | 29 | 31 | 23 | 31 | 43 | 33 | 24 | 28 | 18 | 19 | 19 | 6 | 8 | 8 | 6 | 3 | 3 | 1 | — | 3 | 1 |
| *USHC* | 1 | 1 | 7 | 11 | 19 | 28 | 31 | 38 | 18 | 39 | 22 | 22 | 25 | 18 | 8 | 8 | 7 | 7 | 3 | 4 | 1 | 2 | 1 | — | — | — | — |
| *USHHC* | 2 | 7 | 7 | 13 | 31 | 31 | 31 | 36 | 35 | 41 | 28 | 34 | 27 | 19 | 12 | 6 | 11 | 9 | 5 | 7 | 2 | 1 | — | 1 | — | — | 1 |
| *USDC* | 5 | 10 | 9 | 21 | 42 | 42 | 43 | 43 | 44 | 19 | 22 | 23 | 13 | 15 | 11 | 8 | 5 | 2 | — | 1 | — | 1 | — | — | — | — | — |
| *USDDC* | 4 | 1 | 7 | 10 | 14 | 22 | 27 | 28 | 36 | 36 | 37 | 28 | 23 | 15 | 13 | 11 | 9 | 7 | 1 | 2 | 1 | — | 1 | — | — | — | — |
| *FSC* | 1 | 6 | 9 | 14 | 17 | 29 | 40 | 29 | 26 | 30 | 45 | 38 | 31 | 21 | 31 | 29 | 27 | 13 | 17 | 15 | 18 | 19 | 12 | 14 | 10 | 7 | 6 |
| *FSSC* | 2 | 6 | 8 | 10 | 13 | 29 | 25 | 28 | 34 | 40 | 30 | 37 | 26 | 35 | 26 | 25 | 25 | 22 | 13 | 17 | 10 | 10 | 8 | 4 | 3 | 2 | 4 |
| *FSHC* | — | 2 | 9 | 18 | 20 | 33 | 30 | 28 | 34 | 21 | 35 | 31 | 19 | 24 | 17 | 14 | 14 | 9 | 11 | 14 | 7 | 7 | 8 | 6 | 5 | 3 | — |
| *FSHHC* | — | 7 | 15 | 20 | 36 | 35 | 31 | 52 | 25 | 38 | 18 | 41 | 39 | 30 | 21 | 19 | 30 | 24 | 21 | 22 | 17 | 11 | 8 | 10 | 12 | 10 | 7 |
| *FSDC* | — | 3 | 6 | 6 | 9 | 14 | 24 | 17 | 21 | 23 | 20 | 26 | 28 | 18 | 9 | 16 | 6 | 7 | 8 | 9 | 11 | 4 | 4 | 1 | 3 | 3 | 2 |
| *FSDDC* | 1 | 2 | 8 | 10 | 14 | 23 | 25 | 31 | 32 | 30 | 24 | 40 | 32 | 30 | 32 | 35 | 15 | 15 | 19 | 18 | 16 | 9 | 13 | 15 | 10 | 9 | 5 |

| Series | 28 | 29 | 30 | 31 | 32 | 33 | 34 | 35 | 36 | 37 | 38 | 39 | 40 | 41 | 42 | 43 | 44 | 46 | 47 | 49 | 51 | 52 | 55 | 79 | Total Plants |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *HHC* | 2 | 5 | 1 | — | — | 4 | 2 | 1 | — | — | — | 3 | — | — | — | — | — | — | — | — | — | 1 | — | — | 496 |
| *HHHC* | 1 | 2 | — | 1 | 1 | — | — | — | 1 | — | 1 | — | — | — | 1 | — | — | — | — | — | — | — | — | — | 554 |
| *HDC* | — | 4 | 1 | 1 | 3 | — | 2 | — | — | 1 | — | — | 1 | — | — | — | — | — | — | — | — | — | — | 1 | 376 |
| *HDDC* | — | — | 2 | 1 | — | 2 | — | — | — | — | — | 1 | — | — | — | — | — | — | — | — | — | — | — | — | 498 |
| *DDC* | 1 | 1 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 255 |
| *DDDC* | 3 | — | — | 2 | — | 3 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 331 |
| *DHC* | — | 3 | 1 | 1 | 2 | — | — | — | 1 | 2 | — | — | — | — | 1 | — | — | — | — | — | — | — | — | — | 452 |
| *DHHC* | 2 | — | 1 | 3 | 1 | — | — | 1 | — | — | — | — | — | — | — | — | — | 1 | — | — | — | — | — | — | 538 |
| *USC* | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 530 |
| *USSC* | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 382 |
| *USHC* | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 321 |
| *USHHC* | — | 1 | — | — | — | — | — | — | — | 1 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 399 |
| *USDC* | 1 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 380 |
| *USDDC* | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 333 |
| *FSC* | 2 | 4 | 3 | 6 | 3 | 6 | 1 | 1 | 2 | 1 | 2 | — | — | — | 1 | — | — | — | — | — | — | — | — | — | 586 |
| *FSSC* | 1 | 1 | 3 | 1 | — | 1 | — | — | 1 | — | — | — | — | — | — | 1 | — | — | 1 | — | — | — | — | — | 502 |
| *FSHC* | 3 | 3 | — | 2 | 2 | 1 | 2 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 432 |
| *FSHHC* | 10 | 9 | 5 | 5 | 5 | 4 | 3 | 3 | 3 | — | 3 | — | 1 | — | — | — | — | — | — | 1 | — | — | — | — | 651 |
| *FSDC* | 2 | — | 3 | — | — | — | 1 | 1 | — | — | — | — | — | — | — | — | — | — | — | — | 1 | — | 1 | — | 307 |
| *FSDDC* | 2 | 3 | 3 | 6 | 2 | 1 | — | — | 2 | — | 1 | — | 1 | 2 | 1 | — | 1 | — | — | — | — | — | — | — | 538 |

desired result is to divide the seeds of individual plants. If this be done and if all the lines[4] be represented

[4] Line or pure line is used merely in the genealogical sense.

throughout the experiment by approximately the same number of individuals, we shall not only be sure that like hereditary tendencies went into all branches of the experiment at the beginning, but can feel confident that no material source of error is introduced by a change in the mean hereditary tendencies in either branch of the experiment through the selective elimination (by reason of relative unfitness for the chosen habitats) of certain (differentiated) lines.

These are ideal conditions, quite unattainable among the innumerable difficulties of practical experimentation. Omitting all particulars, I believe we may with reasonable security consider the seeds which went into the original starvation and into the original feeding series random samples from the same individual plants. These lines were maintained with moderate success throughout the experiment.

The following details concerning the methods of manipulating the material may not be irrelevant.

Every seed was, so far as could be determined by inspection, perfectly formed and developed.[5] No seeds in which the coats were sensibly wrinkled were included, since this might indicate either a premature drying of the seed in the pod, or a subsequent wetting.[6]

In harvesting, the plants were left in the field as long as possible to allow the pods to ripen. They were then gathered, and wrapped intact in newspaper to permit any possible translocation of remaining plastic materials from the stems or the pod walls to the seeds.[7]

[5] Every seed was examined at least once. Unfortunately this can not preclude the possibility of a seed containing a weevil which had not emerged up to the time of planting. A large proportion of the seeds planted in these experiments was also weighed individually for use in pure line and other investigations. Of course the seeds giving rise to the plants with which the experiments originated—the *NH, ND, US, FS* and *BG* individuals—form a necessary exception to this rule.

[6] I have carried out no experiments to determine what the real causes are of this wrinkling.

[7] This precaution applies to only two of the original series, to *NH* and *ND,* but not to *FS, US* and *BG.*

## 2. Cultural Conditions

Having prefaced that the purpose of this study is not to determine what chemical and physical factors produce in the individual the effects which we designate as starvation, we are free to choose for the ancestral series any plots which present reasonably extreme conditions of starvation and feeding.

The two fields in southeastern Ohio seemed perfectly adapted to the purposes of the experiment. Their crops of the common Navy beans presented the most diverse appearance. The *H* field—that grown by Mr. Geo. A. Harris bore a moderately heavy crop. The *D* field—grown by Mr. Elmer Dille—seemed to have almost if not quite as good a stand, but the plants were exceedingly small.

The differences were apparently not due to variety, for both were, in so far as could be seen, identical. They were obviously not referable to cultivation, for both had been equally well tended. The differences seemed entirely attributable to the exceedingly poor soil of the *D* field.

Minute description of these two fields is quite unnecessary. They were about a mile apart, and hence under the same general conditions of climate. Neither was level. Field *H* was much longer than wide and sloped from the ends towards the middle, where the ground was apt to be a little too damp. Plot *D* was situated on an exposed ridge where practically all the surface soil had washed away.

The plants originally growing upon these fields formed the starting point for the starvation-feeding comparison. This was in the fall of 1907. In 1908 transfers were made, in order that we might be sure that genotypically, as the pure linist would have it, the plants cultivated on both fields were the same. Other varieties were also added in 1908. These points are made quite clear by the diagrams.

The comparison furnishing the test of the influence of

the $D$ and $H$ conditions upon the offspring should not be made on either of these fields.[8]

Three fields[9] under control of the Station for Experimental Evolution at Cold Spring Harbor were chosen for the comparison. All the Navy series were tested

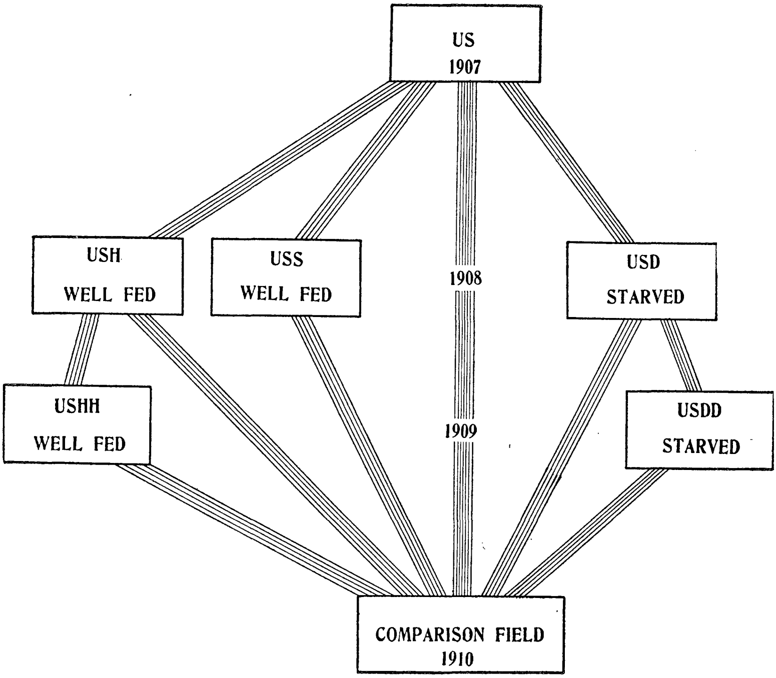



Diagram 2. Cultural history of the Ne Plus Ultra (U) series. The White Flageolet (F) series was subjected to an identical treatment.

on one field and all the Ne Plus Ultra and White Flageolet on another. The third field was devoted to the

[8] A number of breeders hold that among plants there is a gradual adaptation to the substratum; that when plants are transferred from one locus to another there is a "new place effect." If, now, the series grown on the starvation field for two years should from some such process of adaptation be better able to thrive under these conditions than a series newly transferred there from a rich soil, or *vice versa,* the comparison would be an obviously unfair one.

The facts bearing upon this point derivable from our material will probably be discussed later.

[9] Three were selected because accidents of season and culture do occur and it is as unwise to plant all one's experimental seed on a single field as to carry all one's pedigreed eggs in one basket.

fourth variety, *BG*, which must be reserved for a later paper.

The following method was adopted for counteracting the possible hetereogeneity[10] of the fields upon which the plants were grown.

The different strains must be subjected to as nearly as possible a random sample of the conditions afforded by any plot. This end is secured by labeling each seed individually and then scattering those of a particular series quite at random over the field. If, then, certain spots are somewhat more fertile or slightly moister than others, all lines will have equal chances of being represented there. If this were not done an undetected differentiation in the substratum might induce quite deceptive differences in the crops.

In these experiments I did not, unfortunately, work to quite this degree of refinement. For technical reasons, it was desirable to have each of the varieties planted in separate rows. Each seed was placed in an individually labeled envelope and the envelopes of a series thoroughly shuffled. The series were then planted in rows, which were scattered as nearly as possible at random across the field. By this means an almost *but probably not quite* random distribution was secured.

## 3. Collection of Data

The recording of the data from the mature plants was an onerous but relatively simple process.

As noted above, the plants were wrapped individually at harvest time when as nearly dry as they could be

[10] Conditions were not worse than those under which much of the experimental evolution work has been done. At the same time I must frankly confess that to the biometrician the comparison fields left much to be desired. Neither of the three was at all level and consequently not of uniform soil texture, fertility or moisture. They were, however, the best available. In stating that conditions are in defect of those desired by the biometrician, we may perhaps remember that they have the advantage of presenting no experimental artificiality, but of being precisely the sort which would be met in ordinary agricultural practise.

Entirely too little attention has been paid to these matters by experimentalists. Compare, for instance, some suggestions in AMER. NAT., Vol. XLV, p. 686.

allowed to become in the field, and after thoroughly drying stored until they could be studied. They were then placed in a saturated atmosphere for a few hours until the pods could be handled without snapping open, and records made of the number of pods per plant and number of ovules and seeds per pod. The seeds were then stored until thoroughly dried at laboratory temperature and humidity, when they were looked over for weighing. Particulars concerning the various characters will be given in the special sections.

### *D. Methods of Analysis of Data*

#### 1. Pertinent Comparisons

The possibility of an influence of ascendant starvation upon descendant characters is to be tested by a series of comparisons. The number which might be made, and with profit, is so great that space requirements impose a stringent limitation.

A first restriction is effected by basing the comparisons upon the simplest of the statistical constants.

A second limitation is effected by the exclusion of all comparisons showing the relative influence of environmental conditions on different varieties. Possibly this question will be considered in another place. Such inter-racial and inter-varietal comparisons are in this paper quite incidental to those which are strictly intra-racial and intra-varietal.

Finally the comparisons within the varieties must be limited[11] to those which seem absolutely essential to our purposes. The constants for the 40 series are given so that the reader may make any comparison he deems desirable.

In the dichotomous system adopted for these experiments, one branch of the stem material was subjected to

[11] In all we have three distinct varieties represented by 40 series of material—18 of Navy and 11 each of White Flageolet and Ne Plus Ultra. If all the $\frac{1}{2}n(n-1)$ comparisons within each variety were made for the three constants, $A$, $\sigma$, and $CV$, 789 differences and their probable errors would have to be calculated for each character observed.

starvation and the other to feeding. Both ancestral and comparison series allow of two kinds of comparisons, intra-ramal and inter-ramal.

In the first case the comparisons will be made within the same branch of the dichotomous system, *i. e.*, the offspring of the starved parents and starved grandparents will be compared with plants whose parents only were starved, both parents and grandparents being in the direct line of descent.[12]

In these tests the individuals grown on the comparison field bear to each other the relationship of "aunts" and "nieces." Such comparisons are possible where the seed retains its vitality for a number of years. They are open to criticism unless it be known that the age of the seed has no influence upon the characteristics of the plants developing from them.[13]

In the second class, the inter-ramal, are those comparisons between points on different branches of the dichotomous scheme. Here two subclasses may be recognized. In the one the comparisons are between strictly homologous points on the starved branch and on the well-fed branch. The effect of one generation's starvation will be compared with the effect of one generation's feeding. In this case comparisons will be made between "first" and "first" cousins. Or Mendelianwise, all individuals compared will be $F_1$, $F_2$ or $F_n$. Such comparisons will be called direct inter-ramal comparisons.

In the second subclass, the comparisons will be made between different points on the two branches; all com-

[12] In the same manner any one who desires may compare plants whose parents and grandparents were well fed with those whose parents only were well fed. This is not done here for the simple reason that I do not know that the well fed series were grown at an extreme of feeding at all comparable with the extreme of starvation which was possible in these experiments. If they were not, one would expect to find a smaller influence, if any, upon the offspring.

[13] It may have occurred to the reader that a valuable comparison for our purpose could be made within the starvation series by determining, *e. g.*, whether *USDD* whose parents *USD* had been starved, had a lower value for any character than *USD* whose parents *US* were not grown under starvation conditions. Such tests are, however, useless because both edaphic and meteorological conditions may differ from year to year.

parisons will be between ancestral individuals or their offspring belonging to different generations. Such will be called cross inter-ramal comparisons.

The most crucial test is that afforded by the direct inter-ramal comparisons. Both the intra-ramal and the cross inter-ramal comparisons have the disadvantage that the (possible) seed age factor is not excluded. Again, atmospheric (meteorological) factors play a much larger part where different seasons instead of a single season are involved.

Turning to our own available data, we note the following points concerning the comparisons:

Only such comparisons as can be made on the basis of both ancestral and comparison series are discussed, although data for some others, *e. g.*, *NH, ND, US, FS, USC, FSC* are given.

In all cases the differences are taken

Starvation
*less*
feeding

so that when starvation tends to reduce a character the difference bears the negative sign.

If we continue our attention strictly to those within the strain, we have the following inter-ramal comparisons:

| Direct | Cross |
|---|---|
| *HD–HH* | *HD–HHH* |
| *HDD–HHH* | *HDD–HH* |
| *DD–DH* | *DD–DHH* |
| *DDD–DHH* | *DDD–DH* |
| *USD–USS* | *USD–USHH* |
| *USD–USH* | *USDD–USS* |
| *USDD–USHH* | *USDD–USH* |
| *FSD–FSS* | *FSDD–FSS* |
| *FSD–FSH* | *FSDD–FSH* |
| *FSDD–FSHH* | *FSDD–FSH* |

If we go beyond the limits of the populations formed by splitting the seeds of the same individual into two

lots, and consider the Navy *D* and Navy *H* comparable, we get:

| Direct | Cross |
|---|---|
| *DD–HH* | *DD–HHH* |
| *DDD–HHH* | *DDD–HH* |
| *HD–DH* | *HD–DHH* |
| *HDD–DHH* | *HDD–DH* |

## 2. Statistical Formulæ Employed

Methods ample for all the needs of this study are furnished by the simplest of the Pearsonian statistical formulæ. The comparisons in the main are restricted to those based on the mean, standard deviation and coefficient of variation.

These do not fully describe a population, but they furnish more information concerning it than do any other three simple constants, and are sufficient for our purposes. The methods of calculation are now familiar or readily accessible to all biologists. The original data are available for any other comparison, *e. g.*, that based on skewness.

The chief possibility of untrustworthiness in the statistical constants seems to me to lie in a possible biological source of error introduced by growing the comparison series in rows instead of mixing all the individually labeled seeds together and scattering them quite at random over the entire field.[14] If because of the irregularity of the fields, some of the rows were subjected to slightly better and some to slightly poorer conditions than the average, and if the rows of an individual series were not distributed over the field in a perfectly random manner, a slight source of differentiation quite undetectible by the statistician's simple probable error would be introduced. I suspect this to be the case, and consequently our probable errors are perhaps too low *as criteria of the existence of differentiation due to the treatment of the ancestry.*

Fortunately we are not limited to a single comparison,

[14] As an extra precaution half rows were frequently used.

but have several pairs. Any one of these might be wrong in its indication of the influence of ancestral environment because of uncontrollable factors making for heterogeneity on the comparison tract, but as long as these factors differ from series to series in a purely random manner, we shall expect to get trustworthy values by averaging the results for the several comparisons.

This averaging may be done in one or both of two ways. Most easily one may simply note the number of alternative cases, above zero and below zero, and calculate the probable error of either class by the formula

$$.67449 \sqrt{N \times .5 \times .5}$$

since, unless there be an influence of the treatment of the ancestors, the probabilities of differences lying above and below zero are equal. In the second case, the true mean and standard deviation of the series of differences may be obtained and the probable error of the mean difference calculated by the familiar formula

$$E_m = .67449 \frac{\sigma}{\sqrt{N}}.$$

It only remains to say that, except when specified, Sheppard's modification was not applied in the calculation of the moments.

## III. PRESENTATION OF DATA AND COMPARISON OF CONSTANTS

### *A. Number of Pods per Plant in Navy, White Flageolet and Ne Plus Ultra Beans*

The purpose of this section is to present the data for number of pods per plant in three varieties, represented by 40 series and over 21,000 individuals, and to draw the comparisons which may profitably be based upon them. The other characters for these varieties and all of the data for still another variety are reserved for later treatment. This character, which is the most easily deter-

mined of any, is also subject to considerable possibility of error. It is impossible to know from an inspection of the matured plants that some of the pods have not been lost by accident. Another difficulty is introduced by the fact that some varieties of beans have a tendency to make a "second growth" when they are allowed to stand in the field after they are completely ripe. Unless frosts are very late these second growth pods rarely mature. If the plants be allowed to stand in the hope that they will ripen these second growth pods, the normal crop of

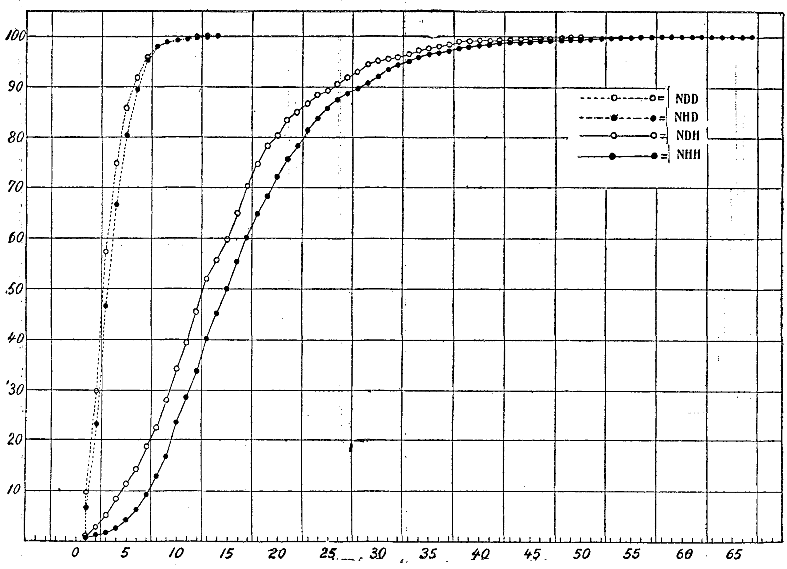
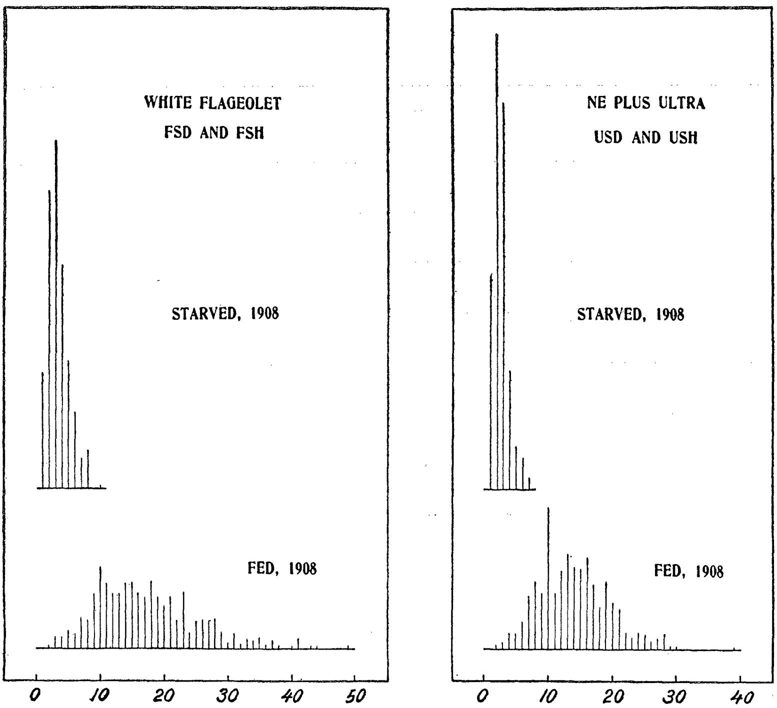



Diagram 3. Number of pods per plant in NDD, NDH, NHD, NHH series. All series are reduced to a percentage basis and the relative frequencies summed from the beginning. The influence of starvation in the reduction of the number of pods is very conspicuous.

pods may either lose their seeds, if the weather be dry, or decay if the weather be wet. All that can be done is to watch the plants carefully, to harvest as soon as practically all the pods that are ripe, and to pull off any second growth sprouts. This apparently introduces a considerable personal equation into the work, but even if true it is unavoidable. I do not believe that a palpable source of error was introduced since ($a$) a large proportion of the plants do not show the second growth at all; ($b$) when

they do, a person with a little practise will make very few mistakes; (*c*) even if errors are made, the treatment is the same for all series.

All the pods counted had at least one matured seed. This specification is necessary since, especially in the autumn, some plants produce quite a number of half developed and completely sterile pods. If these were included there would be no point where a line could be




Diagrams 4 and 5. Percentage frequency of number of pods per plant under starvation and feeding conditions for White Flageolet and Ne Plus Ultra series, 1908.

drawn between the number of flowers and the number of pods produced by an individual.

The record forms do not interest the general reader. The original data are given in Tables *A–C*. The physical constants appear in Tables I–III.

The extreme sensitiveness of the number of pods per plant to environmental conditions is seen at once from an

inspection of the tables of raw data, and better still from the three graphs, diagrams 3–5, for the number of pods per plant in the 1908 series.[15]

We may now summarize as briefly as possible, and largely by diagrams, the results which may be gathered

TABLE I

| Series | Mean and Probable Error | Standard Deviation and Probable Error | Coefficient of Variation and Probable Error |
|---|---|---|---|
| *NH* | 15.2375 ± .4042 | 7.5800 ± .2858 | 49.746 ± 2.294 |
| *NHH* | 16.9919 ± .1518 | 8.6696 ± .1073 | 51.022 ± 0.781 |
| *NHHH* | 11.9308 ± .0977 | 5.1652 ± .0691 | 43.293 ± 0.679 |
| *NHD* | 3.9682 ± .0348 | 1.9433 ± .0246 | 48.972 ± 0.755 |
| *NHDD* | 4.5822 ± .0462 | 2.3756 ± .0327 | 51.844 ± 0.884 |
| *ND* | 2.6782 ± .0335 | 1.1662 ± .0237 | 43.545 ± 1.040 |
| *NDD* | 3.5926 ± .0563 | 1.8917 ± .0398 | 52.657 ± 1.384 |
| *NDDD* | 4.4074 ± .0608 | 1.9329 ± .0430 | 43.855 ± 1.149 |
| *NDH* | 14.6179 ± .2148 | 8.2422 ± .1519 | 56.385 ± 1.330 |
| *NDHH* | 11.8265 ± .1408 | 4.9595 ± .0995 | 41.935 ± 0.978 |
| *NHHC* | 11.9597 ± .2212 | 7.3010 ± .1564 | 61.047 ± 1.728 |
| *NHHHC* | 10.6498 ± .1788 | 6.2390 ± .1264 | 58.583 ± 1.541 |
| *NHDC* | 10.9362 ± .2747 | 7.8970 ± .1943 | 72.210 ± 2.539 |
| *NHDDC* | 10.2851 ± .1845 | 6.1042 ± .1305 | 59.350 ± 1.656 |
| *NDDC* | 9.3098 ± .2259 | 5.3470 ± .1597 | 57.434 ± 2.210 |
| *NDDDC* | 9.9819 ± .2360 | 6.3673 ± .1669 | 63.789 ± 2.252 |
| *NDHC* | 9.9801 ± .2079 | 6.5532 ± .1470 | 65.662 ± 2.010 |
| *NDHHC* | 9.9851 ± .1827 | 6.2839 ± .1292 | 62.933 ± 1.732 |

TABLE II

| Series | Mean and Probable Error | Standard Deviation and Probable Error | Coefficient of Variation and Probable Error |
|---|---|---|---|
| *USS* | 15.7382 ± .1562 | 6.0379 ± .1104 | 38.365 ± 0.798 |
| *USH* | 14.0416 ± .1972 | 5.5542 ± .1394 | 39.555 ± 1.138 |
| *USHH* | 8.4375 ± .1462 | 3.2439 ± .1034 | 38.446 ± 1.250 |
| *USD* | 2.5929 ± .0468 | 1.2265 ± .0331 | 47.300 ± 1.536 |
| *USDD* | 3.6203 ± .0919 | 2.0986 ± .0650 | 57.970 ± 2.322 |
| *USC* | 10.1434 ± .1285 | 4.3846 ± .0908 | 43.226 ± 1.050 |
| *USSC* | 11.7068 ± .1594 | 4.6188 ± .1127 | 39.454 ± 1.102 |
| *USHC* | 9.9844 ± .1541 | 4.0936 ± .1090 | 41.000 ± 1.262 |
| *USHHC* | 10.1103 ± .1564 | 4.6299 ± .1106 | 45.794 ± 1.303 |
| *USDC* | 8.4474 ± .1331 | 3.8477 ± .0942 | 45.549 ± 1.326 |
| *USDDC* | 10.1231 ± .1426 | 3.8579 ± .1008 | 38.110 ± 1.132 |

[15] The 1908 instead of the 1907 series was chosen for these graphical comparisons, since the number of available series is larger—eight as compared with two—and since the number of individuals is much greater, giving much smoother results. The data are available for any similar comparison the reader may care to make. To render the results for all series quite comparable, they have been reduced to a percentage basis. In the first diagram, where data for four series are laid side by side, the percentages have been summed from the beginning for each pod class. In the second and third diagram the percentage frequency of each number of pods per plant is represented by the height of a line.

TABLE III

| Series | Mean and Probable Error | Standard Deviation and Probable Error | Coefficient of Variation and Probable Error |
|---|---|---|---|
| *FSS* | 15.0265 ± .1697 | 7.4134 ± .1200 | 49.335 ± 0.974 |
| *FSH* | 17.2947 ± .2456 | 7.9364 ± .1736 | 45.889 ± 1.197 |
| *FSHH* | 11.8415 ± .1562 | 4.7959 ± .1104 | 40.501 ± 1.075 |
| *FSD* | 3.4252 ± .0552 | 1.6929 ± .0390 | 49.424 ± 1.390 |
| *FSDD* | 4.0362 ± .0593 | 1.7294 ± .0419 | 42.848 ± 1.215 |
| *FSC* | 14.2218 ± .2056 | 7.3804 ± .1454 | 51.895 ± 1.268 |
| *FSSC* | 12.9562 ± .1856 | 6.1678 ± .1313 | 47.605 ± 1.222 |
| *FSHC* | 12.2431 ± .2068 | 6.3729 ± .1463 | 52.053 ± 1.483 |
| *FSHHC* | 14.1505 ± .2115 | 7.9996 ± .1495 | 56.532 ± 1.353 |
| *FSDC* | 12.9055 ± .2616 | 6.7949 ± .1850 | 52.652 ± 1.787 |
| *FSDDC* | 14.4981 ± .2090 | 7.1885 ± .1478 | 49.583 ± 1.245 |

from the tables of constants. As already emphasized the comparisons between the ancestral series are of interest for our present purposes only in so far as they furnish proof that the parents of the comparison series were conspicuously differentiated in type and variability because of the environmental conditions to which they were subjected. The reader must always keep in the foreground the fact that our problem is not to determine in detail what the causes of this differentiation are, but merely to show that a conspicuous differentiation exists and to ascertain whether it has any weight in determining the characteristics of the offspring.

The differences between the starved and well-fed ancestral series are so well marked that constants are best represented by graphs for all the series. In diagrams 6 and 7, which embody data for all possible comparisons for $A$ and $\sigma$, roughly made, the key number of the variety is given along the left-hand margin. The value of the constant for the ancestral series is indicated by the position of a solid dot when the series is a starved one, and by the position of a circle when it is a well-fed one. The value of the constant for the offspring of each of these ancestral series grown upon the comparison field is shown by the position of a solid square under a separate scale. Thus the key to the comparison series is given by adding $C$ to the formula for the ancestral series.

The graphs for the mean number of pods per plant and for the standard deviation of number of pods per plant

brings out with great force and clearness the following facts:

(*a*) The difference between the ancestral series subjected to the *S* and *H* conditions and those subjected to the *D* environment is very great. In all cases means and

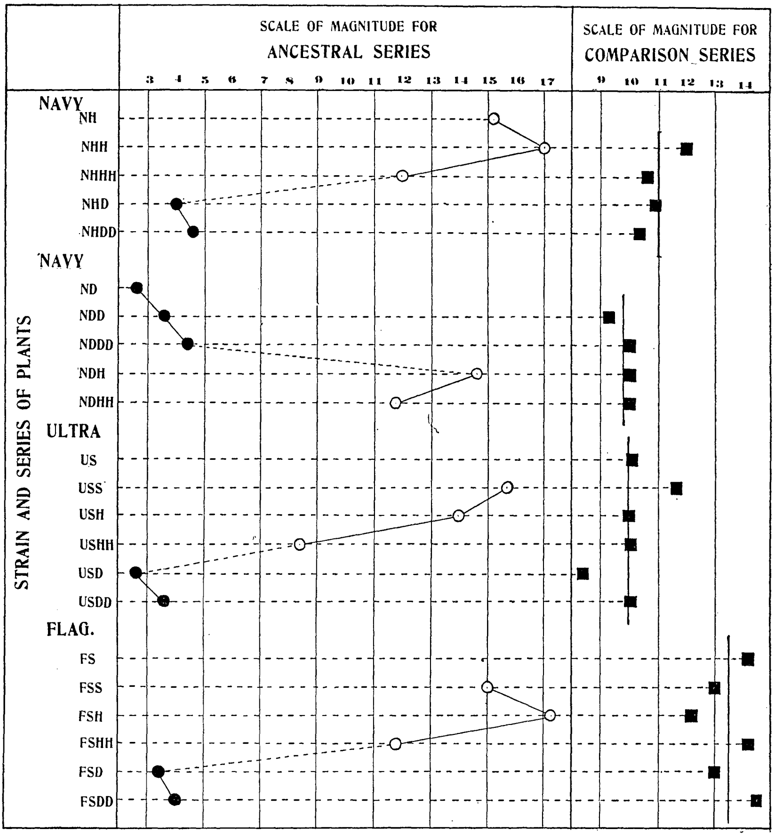



Diagram 6. Mean number of pods per plant in ancestral, or ascendant, series subjected to various conditions of starvation and feeding and in the offspring, descendant, or comparison series subjected to conditions uniform for each strain. Note that the means for the ancestral series vary widely and in direct response to environmental conditions. The comparison series, however, show much smaller differences, and no clear indications of an influence of the ancestral conditions.

standard deviations are conspicuously higher when the plants are well fed than when they are starved.

(*b*) There are considerable differences between a strain grown on the same field in different years.

Season is evidently a large factor in determining number of pods per plant. This is most striking in the means but it is also detectible in the standard deviations. For the means we note that in each of the four strains the average was conspicuously lower in 1909 than in 1908 on the *H* field and slightly higher in 1909 than in 1908 on the

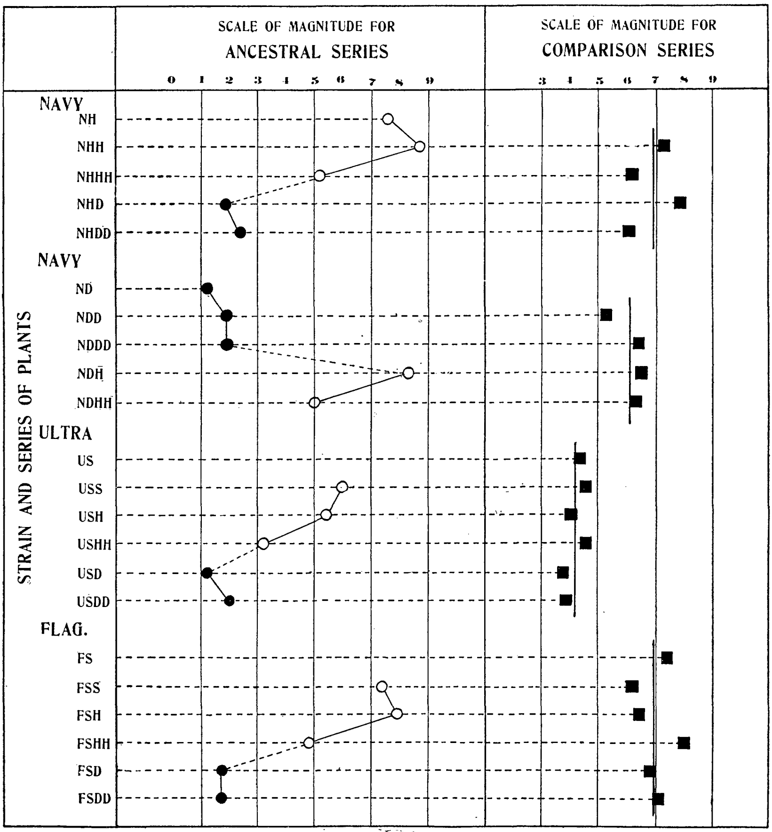



Diagram 7. Standard deviation of number of pods per plant in ancestral and comparison series. Compare the explanation of diagram 6.

*D* field. The standard deviations show precisely the same results for the *H* field, but the differences between 1908 and 1909 for the *D* crops are relatively small.

(*c*) The differences between the comparison series are considerable, but it is impossible to be certain of any influence of the treatment of the ancestors.

(*a*) and (*b*) are facts to be expected from the common experience of all those who have occupied themselves extensively with the growing of plants; they are summarized here merely because it is idle to discuss (*c*) unless the results for (*a*) are clean cut.[16]

Turn now from diagrams to physical constants. Consider first the intra-ramal comparisons, those cases in which individuals whose ancestors have been starved for a longer period are contrasted with individuals in the same line of descent whose ancestors have been starved for a shorter period of time. The necessary constants appear in Table IV.

TABLE IV

| Description of Material | Ancestors Starved for Two Generations | Ancestors Starved for Three Generations |
|---|---|---|
| Ancestors starved for one generation: | | |
| *USDC* series: | *USDDC* series: | |
| Mean | + 1.6757 ± 0.1952 | |
| Standard deviation | + 0.0102 ± 0.1378 | |
| Coefficient of variation | − 7.439 ± 1.743 | |
| *FSDC* series: | *FSDDC* series: | |
| Mean | + 1.5926 ± 0.3348 | |
| Standard deviation | + 0.3936 ± 0.2369 | |
| Coefficient of variation | − 3.069 ± 1.178 | |
| *NHDC* series: | *NHDDC* series: | |
| Mean | − 0.6511 ± 0.3309 | |
| Standard deviation | − 1.7928 ± 0.2341 | |
| Coefficient of variation | −12.960 ± 3.031 | |
| Ancestors starved for two generations: | | |
| *NDDC* series: | | *NDDDC* series: |
| Mean | | + 0.6721 ± 0.3266 |
| Standard deviation | | + 0.9203 ± 0.2311 |
| Coefficient of variation | | + 6.355 ± 3.155 |

Two of these means seem to be significant in comparison with their probable errors, and both of these indicate that starvation of the ancestry for two as compared with one generation, increases the number of pods on the offspring plant. But, it must be remembered that the seed is necessarily a year older for a single generation of starvation only. Furthermore, the series are too few and the differences are entirely too small—only 1.6 pods—to lay particular stress upon it.

The second set of comparisons, the inter-ramal, those

[16] Those noted under (*b*) may be treated more fully later.

between individuals whose ancestors had been subjected to distinctly unlike treatment is made in Tables V–VIII.

Consider first the means. Altogether there are 28 inter-ramal comparisons, direct and cross. The number of pods is smaller in the plants whose ancestors had been starved in 16 out of 28 cases. If there were no relationship between the conditions to which the ancestors were subjected and the number of pods which their offspring produced, one would expect 14 to be negative, providing the errors of random sampling had not to be allowed for. But the probable error is

$$.6745\sqrt{28 \times .5 \times .5} = 1.79.$$

Clearly a difference of $2 \pm 1.79$ has no significance.

If now we restrict the comparison to differences significant with regard to their probable errors, and consider Diff./$E_{\mathrm{diff.}} > 3$ to be significant, we note that only 11 out of the 28 differences may be regarded as statistically trustworthy. Of these, 9 have the negative and only 2 the positive sign. Certainly this looks as though there were a very slight effect of the starvation of the ancestors, but nevertheless an effect quite detectible by the statistical methods.

This point may be tested further by taking the averages, regarding sign, of the pertinent differences for the series of the three varieties. To make sure that slight racial differences between *ND* and *NH* do not obscure the results we recognize two classes of comparisons, within the strain and between strains. The results are:

| | | |
|---|---|---|
| Navy, | Within Strains, | $A = -\ .515$ |
| | Between Strains, | $A = -\ .515$ |
| | General Average, | $A = -\ .515$ |
| Ne Plus Ultra, | | $A = -1.315$ |
| White Flageolet, | | $A = +\ .585$ |

In all cases except the White Flageolet series[17] the number of pods is slightly lower when the ancestors have been starved.

[17] Note also that the two cases of significantly positive differences occur in the White Flageolet variety.

TABLE V

| Description of Material | Ancestors Starved for One Generation *NHDC* | Ancestors Starved for Two Generations *NHDDC* |
|---|---|---|
| Ancestors well fed for one generation: | | |
| *NDHC* series: | | |
| Mean | + 0.9561 ± 0.3445 | + 0.3050 ± 0.2780 |
| Standard deviation | + 1.3438 ± 0.2437 | + 0.4490 ± 0.1965 |
| Coefficient of variation | + 6.548 ± 3.238 | − 6.312 ± 2.604 |
| Ancestors well fed for two generations: | | |
| *NHHC* series: | | |
| Mean | − 1.0235 ± 0.3527 | − 1.6746 ± 0.2881 |
| Standard deviation | + 0.5960 ± 0.2494 | − 1.1968 ± 0.2037 |
| Coefficient of variation | +11.163 ± 3.071 | − 1.697 ± 2.393 |
| *NDHHC* series: | | |
| Mean | + 0.9511 ± 0.3298 | + 0.3000 ± 0.2596 |
| Standard deviation | + 1.6131 ± 0.2332 | − 0.1797 ± 0.1836 |
| Coefficient of variation | + 9.277 ± 3.073 | − 3.583 ± 2.396 |
| Ancestors well fed for three generations: | | |
| *NHHHC* series: | | |
| Mean | + 0.2864 ± 0.3277 | − 0.3647 ± 0.2569 |
| Standard deviation | + 1.6580 ± 0.2319 | − 0.1348 ± 0.1817 |
| Coefficient of variation | + 13.627 ± 2.970 | + 0.767 ± 2.262 |

TABLE VI

| Description of Material | Ancestors Starved for Two Generations *NDDC* | Ancestors Starved for Three Generations *NDDDC* |
|---|---|---|
| Ancestors well fed for one generation: | | |
| *NDHC* series: | | |
| Mean | − 0.6703 ± 0.3071 | + 0.0018 ± 0.3145 |
| Standard deviation | − 1.2062 ± 0.2170 | − 0.1859 ± 0.2225 |
| Coefficient of variation | − 8.228 ± 2.987 | − 1.873 ± 3.019 |
| Ancestors well fed for two generations: | | |
| *NHHC* series: | | |
| Mean | − 2.6499 ± 0.3162 | − 1.9778 ± 0.3234 |
| Standard deviation | − 1.9540 ± 0.2236 | − 0.9337 ± 0.2287 |
| Coefficient of variation | − 3.613 ± 2.805 | + 2.742 ± 2.838 |
| *NDHHC* series: | | |
| Mean | − 0.6753 ± 0.2905 | − 0.0032 ± 0.2985 |
| Standard deviation | − 0.9369 ± 0.2054 | + 0.0834 ± 0.2110 |
| Coefficient of variation | − 5.499 ± 2.807 | + 0.856 ± 2.841 |
| Ancestors well fed for three generations: | | |
| *NHHHC* series: | | |
| Mean | − 1.3400 ± 0.2881 | − 0.6679 ± 0.2961 |
| Standard deviation | − 0.8920 ± 0.2037 | + 0.1283 ± 0.2093 |
| Coefficient of variation | − 1.149 ± 2.694 | + 5.206 ± 2.729 |

Consider now only the ten direct inter-ramal and the ten cross inter-ramal, forming the twenty possible intra-varietal comparisons. Of the ten direct intra-ramal comparisons which are available from the four series, seven have the negative and three the positive sign. In two cases only is Diff.$/E_{\text{diff.}} > 3$, and in one case $> 2.5$.

TABLE VII

| Description of Material | Ancestors Starved for One Generation *USDC* | Ancestors Starved for Two Generations *USDDC* |
|---|---|---|
| Ancestors well fed for one generation: | | |
| *USSC* series: | | |
| Mean | − 3.2594 ± 0.2076 | − 1.5837 ± 0.2138 |
| Standard deviation | − 0.7711 ± 0.1470 | − 0.7609 ± 0.1513 |
| Coefficient of variation | + 6.095 ± 1.724 | − 1.344 ± 1.579 |
| *USHC* series: | | |
| Mean | − 1.5370 ± 0.2037 | + 0.1387 ± 0.2100 |
| Standard deviation | − 0.2459 ± 0.1442 | − 0.2357 ± 0.1483 |
| Coefficient of variation | + 4.549 ± 1.830 | − 2.890 ± 1.695 |
| Ancestors well fed for two generations: | | |
| *USHHC* series: | | |
| Mean | − 1.6629 ± 0.2054 | + 0.0128 ± 0.2117 |
| Standard deviation | − 0.7822 ± 0.1453 | − 0.7720 ± 0.1497 |
| Coefficient of variation | − 0.245 ± 1.859 | − 7.684 ± 1.726 |

TABLE VIII

| Description of Material | Ancestors Starved for One Generation *FSDC* | Ancestors Starved for Two Generations *FSDDC* |
|---|---|---|
| Ancestors well fed for one generation: | | |
| *FSSC* series: | | |
| Mean | − 0.0507 ± 0.3208 | + 1.5419 ± 0.2795 |
| Standard deviation | + 0.6271 ± 0.2269 | + 1.0207 ± 0.1977 |
| Coefficient of variation | + 5.047 ± 2.165 | + 1.978 ± 1.744 |
| *FSHC* series: | | |
| Mean | + 0.6624 ± 0.3335 | + 2.2550 ± 0.2939 |
| Standard deviation | + 0.4220 ± 0.2358 | + 0.8156 ± 0.2078 |
| Coefficient of variation | + 0.599 ± 2.322 | − 2.470 ± 1.936 |
| Ancestors well fed for two generations: | | |
| *FSHHC* series: | | |
| Mean | − 1.2450 ± 0.3365 | + 0.3476 ± 0.2973 |
| Standard deviation | − 1.2047 ± 0.2379 | − 0.8111 ± 0.2102 |
| Coefficient of variation | − 3.880 ± 2.241 | − 6.949 ± 1.838 |

All these are negative. There are no statistically significant positive differences, the actual values being .013 ± .212, .348 ± .297, and .662 ± .334. The two larger of these occur in the White Flageolet series. The mean for the ten direct comparisons is —.589 pods.

Of the ten cross inter-ramal comparisons, five are negative and five are positive; six are significant with regard to their probable error, four with the negative and two with the positive sign. In both cases of positive differences (*i. e.,* where the seeds from starved ancestors produced more pods than those from fed ancestors) the seed from the fed plants was a year older than that from the starved plants. The average for the cross comparisons is —.262 pods.

Consider the standard deviations.

As already noted, and as is clearly to be seen from the graph, the standard deviations for the starved and fed ancestral series show differences agreeing in general with those seen in the means. This is to be expected, since $A$ and $\sigma$ are generally closely correlated. For this reason it is idle to discuss the influence of starvation or feeding upon variability on the basis of the standard deviation alone.

Turning to the comparison series, we note that of the 28 differences, taken altogether, 17 are negative and 11 positive. The deviation from expectation is therefore $3 \pm 1.79$, and can not be asserted to be significant.

Again taking Diff./$E_{\text{diff.}} > 3$ as indicating differences significant with regard to the errors of sampling, we note that 17 cases out of 28 are statistically significant. Of these 17 cases, 12 are negative and 5 are positive. Consider averages as before:

| | | |
|---|---|---|
| Navy, | Within Strains, | $A = -.165$ |
| | Between Strains, | $A = -.053$ |
| | General Average, | $A = -.109$ |
| Ne Plus Ultra, | | $A = -.595$ |
| White Flageolet, | | $A = +.145$ |

Again limiting comparisons to the strictly intra-varietal, and segregating into direct and cross inter-ramal comparisons, we find that of the ten direct comparisons possible in the four lots, six are negative and four positive in the sign of the difference. Only four are statistically significant, *i. e.*, Diff./$E_{\text{diff.}} > 3$, and all are negative. The average is $-.221$. Of the ten cross inter-ramal comparisons, seven are negative and three are positive in sign; with regard to their probable error, eight are significant; of these five are negative and three are positive. The mean for the series is $-.181$.

Note the following points concerning the relative variabilities as expressed by the coefficients of variation.

Taken altogether, fifteen differences are negative and thirteen are positive in sign. Accepting a difference of

three times its probable error as statistically significant, we note that altogether only six out of the twenty-eight differences may be regarded as trustworthy. Of these four are positive and two are negative in sign. Taking means as for the two preceding constants, we find:

| | |
|---|---|
| Navy, Within Strains, | $A = + .912$ |
| Between Strains, | $A = + .912$ |
| General Average, | $A = + .912$ |
| Ne Plus Ultra, | $A = -.253$ |
| White Flageolet, | $A = - .946$ |

With mean differences as slight as these, one certainly can not argue that the starvation of the parents has had any pronounced influence upon the relative variability of the offspring.

## PROVISIONAL SUMMARY

1. The foregoing pages are devoted to a statement of problems, description of methods and the presentation of a first part of the data secured in a biometric investigation of the influence of the starvation of the ascendants upon the characteristics of the descendants in garden beans. Since several months will necessarily elapse before all of the materials can be worked up, it has seemed undesirable to withhold the constants already calculated and checked, viz., those for number of pods per plant in three varieties represented by forty series comprising altogether about 21,000 individuals. The publication is therefore partial but in no sense preliminary. Several questions that might be discussed on the basis of the data presented are passed over until more series of material can be lined up. The conclusions drawn—even for number of pods per plant—are provisional merely.

2. The purpose of this research was not to ascertain the physico-chemical factors to which starvation is due, but to determine whether such artificial depauperization of the ancestors has any influence upon the characters of the offspring. Such ordinary "fertile" and "sterile" or "good" and "poor" agricultural land was therefore

taken for the ancestral series as would produce moderately extreme conditions of depauperization and luxuriance in the crops.

3. The influence of from one to three generations starvation of the ascendants upon the characteristics of the adult descendants is not conspicuous, in fact hardly to be detected by the eye in the field. Statistical constants *seem,* however, to show a slight yet unmistakable influence of the treatment of the ancestors in the form of a slight decrease in the number of pods per plant.

4. The published data are as yet insufficient to justify any discussion of the question of the cumulative influence of the starvation conditions, or of the mechanism through which the characters of the offspring plants are modified. Evidence on these and various other pertinent questions are being gathered as rapidly as possible.